

Interactive comment on “Influence of tree size, taxonomy, and edaphic conditions on heart rot in mixed-dipterocarp Bornean rainforests: implications for aboveground biomass estimates” by K. D. Heineman et al.

K. D. Heineman et al.

kheineman@life.illinois.edu

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Dear Editors,

We thank you for the opportunity to publish our manuscript (“Influence of tree size, taxonomy, and edaphic conditions on stem rot in mixed-dipterocarp Bornean rainforests: implications for aboveground biomass estimates”) on the Biogeosciences Discussions Forum. We are also grateful to the reviewers for providing detailed feedback that will undoubtedly improve the quality of our study. Below, we respond individually to each

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point raised by the reviewers, and describe the changes that have been made to the manuscript or that we are willing to make as a result of these suggestions. Page, section, and line numbers noted in our responses refer to the original manuscript unless otherwise noted. We have attached a Response Supplement, which includes supporting tables and figures referenced in the comments below.

We are happy to make further modifications if needed.

Sincerely,

Katherine Heineman, on behalf of all co-authors

Reviewer #1

1. “Having said that, there is some room for improvement because some methodological points need some more detail. For example, the drilling method is not described clearly enough, i.e. what size (diameter) drill was used (and make of the drill itself, or would any drill suffice?), and was drilling always continued until the centre of the tree, or stopped at a certain depth (perhaps depending on the length of the drill). This is important info because the drilling method is probably the easiest and most reliable method of detecting stem rot after felling, so people (like myself) may probably like to use this method.”

Response: We regret if aspects of the drilling methodology were not clearly described. To clarify the this procedure, we have added the following details to section 2.2: 1) the diameter of the drill bit was 1.5 cm and 2) each hole was drilled to a depth equal to one half of the DBH of the tree, or until the presence of stem rot was identified by visual inspection.

The manufacturer of the drill was not recorded. Given that the field data collection for the Central Sarawak site occurred 40 years ago, the exact drill model is unlikely to be available for future field studies.

2. “Also because tree identify was the main factor determining wood rot severity and

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biomass loss, it would be good to have a list of tree species sampled with the observed values of wood rot frequency, intensity and biomass loss due to rot. This maybe useful to find associated species traits that can explain these observations.”

Response: We agree with Reviewer #2 that including a table of species-specific stem rot frequency and severity values would make this article more useful for future researchers. Such a table was originally omitted for the sake of brevity and because we had planned to write a companion paper focused on the taxonomic variability in stem rot. However, we have now created a table listing species covariates used in generalized linear models along with species mean stem rot severity (from the felling dataset) and stem rot frequency in each of the three datasets (drilling, felling and coring). This table can be added as supplementary material.

This supplemental table may help to dispel any confusion about the level of taxonomic resolution in the drilling and felling datasets. Nearly all of the trees at the Central Sarawak site were identified to species, including 93% of trees felled and 79% of trees drilled (counts listed in Table R1 (Response Supplement); also see section 2.1 (page 8 line 1) in the original manuscript (MS)). The degree of taxonomic certainty is higher in the felling dataset than the drilling dataset because close inspection of botanical characters for identification was afforded by felling the tree. However, the taxonomic precision in the drilling dataset is perhaps the best that can be expected for field identification in this hyper-diverse Bornean rainforest, which has the highest species richness on record in the Paleotropics. Trees in the coring data were not in the Lambir 52-ha plot, since such destructive sampling is not permitted there. Instead, trees were located by relatively systematic searching of the surrounding areas with the same soil types as found in the 52-ha plot. For each tree in the coring dataset, we collected voucher specimens, which were identified to species by co-author Sylvester Tan who is the chief botanist of the Lambir 52-ha plot employed by the Center for Tropical Forest Science. We believe that the confusion about the taxonomic resolution was perhaps created by the inclusion of three genera in Figure 3, which was intended to illustrate the

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difference among common taxa in stem rot frequency and severity. We have modified in the legend of this figure to read as follows: “Variation in the frequency and severity of stem rot among important dipterocarp genera in rain forest of Central Sarawak, Borneo, which represent a subset of the 65 genera felled in the logging inventory.”

3. “Abstract: Although I understand that the authors want to emphasize the new findings in the abstract, i.e. the influence of soil properties on stem rot, the main finding of this study remains that species identity is by far the most important factor! It could even have influenced (indirectly via species compositional patterns) the detected soil impact on stem rot. Therefore I think that emphasis has to be on the impact of species identity on stem rot. This will confirm the importance of including species traits (other than wood density) in estimating forest biomass values.”

Response: To better emphasize the importance of species-specific effects, we have modified the final sentences of the abstract as follows (page 3 line 23): “This study demonstrates not only that stem rot is a significant source of error in forest carbon estimates, but also that it strongly covaries with tree taxonomy and soil resources, underscoring the need to account for tree community composition and edaphic variation in estimating carbon storage in tropical forests.” To address the taxonomic controls over stem rot in more detail, we suggest that our linear model analysis of the effect of genus on stem rot (section 2.5 page 11 line 5) be superseded by a nested analysis of variance evaluating the relative importance of family, genus, and species on the frequency and severity of stem rot, as has been done in other trait-based studies in diverse tropical forests (e.g. Fyllas et al. 2009). Reviewer #1 also makes an excellent point that the variation among species in stem rot is an important example of species-level controls over biomass storage, which are often ignored in ecosystem studies. In the Introduction, we now emphasize the point that using a trait-based approach to identifying species-level correlates of stem rot incidence could improve understanding of the global carbon cycle, as suggested by Cornwell et al. (2009) in relation to trait-driven fates of wood relevant to biogeochemical cycles in ecosystems. Given that

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species identity was by far the most important model covariate in the variance partitioning analysis, there are clearly other aspects of species identity beyond the species covariates evaluated here (wood density and soil association) that are important for explaining variation in stem rot frequency and severity, and we raise these in the Discussion. For example, species differences in wood chemistry may be relevant, as wood N has been shown to vary widely among species in tropical forests (Martin et al. 2014) and species wood nitrogen and C:N ratios are important correlates of wood decomposition rates (Weedon et al. 2009). We also rearranged the order of the discussion to list the taxonomic factors (currently section 4.3) before the soil effects (currently section 4.2) to reflect their relative importance to predicting rot.

We do not feel that our emphasis on soil factors was unwarranted, given that the soil variables were significantly associated with stem rot in linear models and in the stand level analysis. And, as Reviewer #1 points out, the soil aspect was a novel part of our manuscript. To better motivate why the focus on soils is important, we have modified the Introduction with to emphasize the importance of accounting for soil resource availability in global biomass estimation (e.g., Yang et al. 2014).

4. "Methods: Chapter 2.2 Its a bit confusing that the species and stem numbers mentioned in the first three lines of chapter 2.2 differ from the ones mentioned in the reference to Table 1. It may be good to explain in the legend of Table 1 that this table only shows a selection of stems from a much larger database of stems (and mention the selection criteria)."

Response: We have revised Table 1 (shown in the Response Supplement) to reflect the total number of trees and species sampled in each dataset and also the number of trees and species included in each mixed effect model. We also modified the number of trees and species collected on section 2.2 to reflect the total number of trees cored, rather than the number used in the linear model. To clarify, all trees in the felling dataset were included analysis of stand-level stem biomass lost to stem rot (Lossmax). However, trees without species-level covariates (wood density or soil habitat associa-

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tion) and information on soil properties could not be including in the GLMMs, nor could trees be included in GLMMs if they were not identified to species, since we included species identity as a random effect in our models (Table 1). The sample sizes of trees included in each model have changed based on the suggestion by Reviewer #2 (see the response to comment #31) to include species for which there fewer than five individuals in a dataset. Upon revision, we will also remake Fig. 2 and 3 to reflect the sample sizes of the complete dataset.

5." Also in chapter 2.2 the term commercial logs is introduced. It says this is based on the diameter and the length of the bole. However, does it also include a taxonomic component? In Bornean forests, mostly dipterocarps are logged commercially, i.e., I like to know if 1) all stems with the suitable dimensions were felled, or 2) only a commercial subset of species (like dipterocarps) were felled and not other species.... Please make this clear in the text as it may influence the outcome of the study."

Response: There was not an explicit taxonomic component in the selection of trees in the felling dataset. As was mentioned in section 2.2 page 8 line 1, the Central Sarawak felling data set included 1035 trees in 240 species in 31 families, showing that the sampling included many other families besides the Dipterocarpaceae. FIDP was a management inventory to assess timber resources for logging and marketing. At the time, much of the output from Sarawak mixed-dipterocarp forests went for peeling and plywood and laminates, and the peeling machines were 12 feet (3.65 m) wide. Hence, there was an emphasis on tree sizes producing "commercial logs," which were defined as 12 feet long with a minimum diameter of 12 inches (see page 8 line 11 of the original MS). We have modified the description of sampling section 2.2 to read: "On a random subset of 44 clusters, all trees, regardless of species, that would produce at least one commercial log (i.e., 3.65 m long with minimum diameter at breast height (DBH) of 30 cm) were felled at breast height (1.3 m) or above the highest buttress head and cut into 3.65 m logs along the length of the stem until the point of first branching or crown point (Fig. S2)"

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There may have been a minor taxonomic role in the exclusion of extremely hardwooded trees (section 2.2 page 9 line 4, see also response to comment #25). However, all three datasets contain extremely broad ranges of tree taxa and wood density values (Table 1), giving our data sets ample power to make inferences about the importance of species identity and wood density in stem rot frequency and severity.

6. "As the stem rot was determined as part of a bole (i.e. not the whole tree), how do you scale this up to whole tree estimates (like is done in the discussion). I didn't see any methodological explanation for this. The bole only represents an obviously important fraction of the whole tree biomass, but not all of it...."

Response: In this paper, we do not attempt to extrapolate stem stem rot estimates to generate whole tree estimates of biomass lost to stem rot, since rot in other parts of the trees, such as in the crown or root, were not quantified. Lossmax is defined in section 2.7 page 13 line 3 as the maximum percent of stem biomass lost to stem rot. To make this distinction more apparent, we added the word "stem" where biomass loss is referred to elsewhere in the methods and in all relevant figures and tables. Mean Lossmax was 10% across spatial clusters analyzed, a detail that has now been added explicitly to the results section 3.3 and discussion in section 4.4. In the discussion, we use the estimate that 70% of aboveground biomass is in tree boles > 30 cm DBH (Yamakura et al. 1986) to arrive at the conclusion that 7% of forest aboveground biomass is affected by stem rot decay in the stems of trees > 30 cm DBH (10% of 70% = 7%). Crown and butt rots are not within the scope of our study, and we know of no other study that has examined crown or root rot, so we could not generate tree-level estimates from the data available. To reduce confusion, we plan to replace all mentions of "heart rot" with "stem rot" in the revised version of the manuscript to more precisely describe what was measured in this study.

7. "The selection criteria for inclusion of trees in the felling, drilling and coring methods remain to vague, please make this clearer. For felling, make clear what a commercial log is, for drilling make clear how many additional stems were added to the felling data

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base and how they were selected, and for the coring explain more about the spatial, diameter and species selection criteria.... Were the cored trees selected at random, were they placed within a plot, inside or outside the CTFS plot, etc...."

Response: We have modified the sampling description in section 2.2 to more clearly reflect the total number of clusters in the FIDP inventory and the proportion used for drilling and felling. To wit, the FIDP conducted a forestry inventory of 502 clusters. On a subset of 44 clusters, all trees that could produce at least one commercial log were felled. A drilling program was implemented on an additional 26 of total clusters, which expanded the dataset to including 1361 additional trees. A total of 419 trees were both drilled and felled to validate the effectiveness of drilling in detecting stem rot. The following information about species selection in the coring dataset has been added to section 2.2: "The stem rot data from Lambir were collected from 361 trees (114 species in 35 families; Table 1) with a 5-mm increment hand borer, bored to half of the DBH. Trees > 6 cm DBH were identified for coring outside of the 52-ha plot, but within approximately 1 km of the plot boundary. We focused sampling on two broad soil habitats, sandy loam and clay. Soil type identification was guided by sampling on areas adjacent to known areas of clay and sandy loam soil inside the 52-ha plot, and soil types were verified by visual inspection of soil characteristics and floristic variation. Within each soil type, trees were cored opportunistically based on field identifications by S. Tan. Voucher specimens were collected for all trees, and field identifications were validated by comparison with herbarium specimens at Lambir Hills National Park by S. Tan. We cored three individuals for most species, although intensive intraspecific sampling (> 16 individuals) was conducted for five common species (*Dryobalanops aromatica*, *Dipterocarpus globosus*, *Macaranga beccariana*, *Vatica micrantha*, and *Dryobalanops lanceolata*). Secondary xylem from extracted cores was examined for stem rot as above, and presence or absence of stem rot was recorded. "

8. "Also give more info on the tree identities. It seems clear from the text that the felling and drilling data set had limited taxonomic resolution (i.e. lumping whole groups of

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species in broad categories like "red meranti" and so on), while the coring data base seems species specific.... Provide more information on this as it is vital for understanding the detected patterns of stem rot...."

Response: As mentioned in the response to comment #2, we are happy to provide a table listing the attributes of each species included in this study. The majority of trees were identified to species in each dataset (Table R1).

9. "Chapter 2.4 The soil associations of the tree species is based on species specific data (I presume). However, the felling and drilling data sets consists of species groups, not individually identified species (I deduct, because it is not clearly described, see previous comments), so how were these two linked?"

Response: Please see the response to comment #2 and Table 1: only trees identified to species were included in the GLMMs for all three datasets.

10. "Also, the Lambir plot has data on trees with dbh \geq 1 cm, while the Potts data made use of trees with dbh \geq 10 cm.... So was there a diameter cutoff used to determine species habitat associations? If not, the CTFS plot data may disproportionately affect the results of this classification as it has many more stems included due to the small diameter cutoff.... If this is true, than the soil association classification may not be so generally applicable as it is suggested, as it may mainly reflect the pattern observed in one particular plot in Lambir...."

Response: As Reviewer #2 suggests, it is true that many species classifications were based on the statistical association of trees to the four main soil types at Lambir. However, there is dramatic variation in soil chemistry among soil types at Lambir generating strong floristic contrast among soil types, patterns that are also observed at larger regional scales, and soil-based habitat partitioning is a defining feature of the forests in this region (Ashton 1964, 1969, 1973, 2015; Baillie et al. 1987). Additionally, the soil environment of trees at the Central Sarawak site (drilling and felling datasets) differs significantly among the Lambir-defined soil habitat groups (Figure R1-Response Sup-

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plement). In particular, trees designated as fine loam/clay specialists are typically found on soils with higher values for soil PC2 (which is positively correlated with soil pH and soil reserve Ca, K, Mg, and P) and lower values for soil PC3 (which is negatively correlated with soil exchangeable Ca and Mg), indicating that species aggregated to high fertility soils at Lambir also prefer high fertility soils in Central Sarawak. Furthermore, the soil habitat associations used in our analyses were verified by Peter S. Ashton, a co-author on our paper and a botanist who is an expert on plant species distributions in the region (see Ashton 1964, 1969, 1973, 2015).

11. "Chapter 2.5 The soil classification used for the coring data set seems not very precise, and its classification is also not well defined (described). This may be a main reason why stem rot showed no response to soils in the coring data set"

Response: The soil classifications at Lambir are discrete rather than continuous, as these soil types are distinct in terms of nutrient concentrations and texture. Moreover, tree species distributions are strongly correlated with these categorically-defined soil types. All of this has been well established by a number of previous studies cited in our manuscript (Baillie et al. 1987; Davies et al. 2005; Baillie et al. 2006; Tan et al. 2009). In the response supplement, we present Table R2 comparing the soils at Lambir and Central Sarawak, which can be added to the supplement. Given the strong covariation in soil chemistry and species composition between soil types, we suspect that the main reason why we do not detect difference among soil types in the Lambir dataset is because of the smaller number of large trees sampled in it (Figure R2 Response Supplement; Table 1 and Fig. 2 in original MS). Only 25% of cored trees were >30 cm DBH, whereas the majority of individuals in the felling and drilling datasets exceeded this threshold. Therefore, because stem rot frequency increases strongly with DBH, we likely have less power than in the drilling and felling datasets to detect variation in stem rot frequency due to soil type because stem rot was observed less frequently due to under-representation of larger trees in the coring dataset. To emphasize this point we have added the following text to the discussion section 4.2: "In

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the coring dataset, the relatively small sample size of large trees may have prevented us from detecting differences in the frequency of stem rot among soil types at Lambir, underscoring the need for stem rot sampling designs to adequately sample up to the largest sizes of trees of a species” The coring data are nonetheless valuable because they illustrate that DBH is an important predictor of stem rot and allow a comparison of the effectiveness of alternative methods for detecting stem rot.

12. “Chapter 2.6 It may be better to move this to the end of the method section, i.e., switch with chapter 2.7, to make the story more readable.”

Response: We chose to order the analysis of stem rot frequency and severity in individual trees (2.6) before the analysis of the stand-level implications of stem rot (2.7) because the latter represents an aggregation of tree level patterns.

13. “Chapter 2.7 Here some info could be given on how to convert the biomass loss observed for logs into biomass loss of the whole tree and forest.....”

Response: See the response to comment #6

14. “Results Chapter 3.1 It remains unclear throughout the manuscript why coring would produce such different estimates from felling and drilling, especially as coring is almost identical to drilling (I would think).... What is causing this discrepancy? Is it really just a methodological issue or is something else going on?”

Response: It is likely that there is a methodological difference in the effectiveness of rot detection between coring and drilling because drilling was evaluated at two points on the stem and coring was evaluated at only one point, as mentioned in the discussion on page 20 line 6. However, we suspect the discrepancies in the results of coring vs. the felling and drilling analyses are also related to the difference in the size distribution of trees measured (see Figure R2 and the response to comment #11).

15. “How do you explain that there is no genus impact on stem rot in the coring data set? Would this be due to the larger groupings used in the felling/drilling data sets? I

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think these differences may stem from different levels of tree identification.....”

Response: The coring dataset included a relatively small number of large diameter trees compared to the drilling and felling dataset (See Figure R2). Because stem rot is much more prevalent in large size classes, our ability to detect differences among genera in the coring dataset is likely limited by the smaller number of individuals demonstrating rot. As mentioned in the response to comment #2, the level of taxonomic resolution very high in all three datasets, so this was most likely not the reason for the difference.

16. “I also don’t understand why drilling and felling find a different impact of Wood density on the presence of stem rot.... Perhaps high wood density stems were excluded from drilling? I.e. again the selection criteria of trees may be important, hence it is crucial to describe these selection criteria in more detail.....”

Response: We suggested in the discussion that differences in methodology and in the size of trees sampled may have generated differences among datasets in the significance of covariates. With respect to methodology, we wrote on section 4.1 page 19 line 21 that validation of the drilling method showed that drilling is fairly accurate for trees with high stem rot severity, but has a higher frequency of false negatives when rot severity is low. Therefore, given that the felling is far less likely to miss unlikely to miss small amounts of rot, compared to the drilling method, the results of analyses of the felling dataset should be interpreted slightly differently than the drilling dataset. It is possible that the necessary exclusion of trees unsafe to fell (see response to comment #7) could have contributed to these effects. However, given the large range of wood density and wide variety of taxa that were included in both drilling and felling datasets, we view this as improbable.

17. “Due to the grouping of species in the drilling and felling data sets, I don’t really trust the soil association outcomes....”

Response: Please see the response to comment #2. There was no grouping of

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species.

18. "Chapter 3.2 PC3 in table 3 is reported as significant in the text, but is not in table 3...."

Response: We corrected this typographic error: the probability listed for soil PC3 in Fig 3 should have been 0.006 rather than 0.06.

19. "Overall, the result section can be shortened.... There were also several where the results were discussed in the result section... This should be removed."

Response: We agree that the discussion could be written more concisely and will make a concerted effort to reduce any repetition of the results upon revision. When findings were discussed a bit in the results section, it was done in order to provide some indication of the implication of the result, in order to increase understanding and clarity of the results, but in revision we will ensure that any such syntax falls short of actual interpretation of results in the Results section.

20. "Discussion Chapter 4 As with the abstract, I think the authors should emphasize their main finding more, i.e. the importance of species specific properties on stem rot...."

Response: Please see the response to comment #3.

Reviewer #2

21. "The methods lack key information necessary for interpreting the results. First, interpretation of the reported frequencies of heartrot depend critically on exactly what part of the stem is investigated for heartrot, which is not clear for either the felling or drilling method."

Response: In the felling dataset, stem rot frequency and severity was evaluated over the whole length of the stem. To clarify this point, we added to the methods section 2.2 the detail that trees were felled at breast height and then cut into 12-foot (3.65 m)

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logs along the length of the stem point of first branching. As stated previously in this section (page 8, line 13), "Presence or absence of stem rot was recorded based on visual inspection of the log ends, and stem rot was scored as present when the wood contained voids or areas of darkened, soft, or brittle wood (Fig. S2). Logs that were sound at one end but rotten at the other were sawn in half to better quantify rot severity." For the drilling method, it was stated that in section 2.2 (page 8, line 23) that each tree was "drilled at 1.3 m perpendicular to the stem axis, with two drill holes at right angles to each other." Therefore, for drilling the stem was evaluated at just one point on the stem, which may explain in part why the frequency of stem rot was greater in the felling than the drilling dataset, as is stated in the discussion section 4.1 (page 19, line 23): "The majority of misclassifications likely occurred because drilling tested for areas of wood softness only at breast height, missing rot occurring higher up in the stem." Also see the responses to the comments above concerning clarification of methods. 22. "The drilling method description does not state the diameter of the drill hole, or the depth to which the log was drilled."

Response: Please see the response to comment #1.

23. "And for the felling method, given that stem rot is examined in the ends of felled logs, it is critical to know the length to which logs were cut."

Response: Felled trees were cut in 12-foot (3.65 m) logs along the length of the stem until the point of first branching (information now included on in section 2.2), and then sawn in half where rot was present at one end but not the other, as mentioned in the original MS in section 2.2 page 8 line 16.

24. "Second, a clear description of the sampling designs for choosing trees is also necessary to interpret the results. This is given only for the drilling dataset. No sampling design is given for the coring dataset at all."

Response: See the response to comment #7.

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25. "For the felling dataset, information on how candidate trees were selected is quite clear, but then it is noted that trees were excluded in the field for safety reasons, and no information is given on the proportions of trees excluded. At the least it should be possible to state the total proportion excluded; ideally there would be numbers by reason for exclusion, size class, etc."

Response: Of trees that met the size requirement for felling (one commercial log), < 20% of trees were excluded either for safety reasons or because they were from timber classes that were very hard to fell, as judged by the forestry crew of the FIDP. The reason that stems were excluded was not recorded at the time of the logging, but the proportion was about equal between these two reasons for exclusion. We have added the proportion of stems excluded to the methods section 2.2. Trees were felled consistent with the forestry objectives, which limits the sampling design but does not diminish the value of this study. The extensive observational dataset presented here includes over 1000 felled trees, and, therefore, provides valuable insight into the patterns of stem rot in tropical forests, a subject that is sorely lacking data. For comparison, Brown et al. 1995, which addresses uncertainty in tropical forest biomass estimates and has been cited 256 times, presents a stem rot biomass correction based on observation of 50 stumps found along the side of a forestry access road. Our data set massively exceeds this in terms of the number of trees, species, and families represented, as well as the quality of the methods used for the estimation of stem rot presence. Moreover, our study examined mixed dipterocarp forests, which are known to have higher biomass per unit ground area than most other tropical forest types (Banin et al. 2014), and so estimation of stem rot is critical to improved estimates of their capacity to store carbon. Consequently, the analysis presented here has broad appeal to the large community of scientists working on tropical forests and global carbon dynamics.

26. "Third, to interpret the soils results, it is important to know how the soil classification in the coring dataset relates to the soils measurements in the other datasets, and also to know how many missing values were interpolated in the latter dataset."

C3955

Response: Please see the response to comment #10, which shows that the tree species associated with different soil types at Lambir also inhabit contrasting soil environments in central Sarawak. We can include this graph in the revision if it alleviates the concern of extrapolating associations quantified statistically at Lambir to the central Sarawak site. We point out, again, that all soil associations were verified by Peter S. Ashton, who is an expert on the botany of Southeast Asian forests and the soil habitat associations of the tree species within them (see page 10 line 6).

In total, 10% of soil values (962 of 9890) were imputed, which is considered a reasonable proportion of missingness. Of these, 72% missing values were subsoil values that had corresponding measures in the topsoil. Sparse missing values were most common for total nitrogen, organic content, and cation exchange capacity. Given the high covariance among soil chemical values, the `areglImpute` function is able to create a realistic distribution of each missing value based on the present variables in the same row. In addition to increasing power of statistical analyses on datasets with sparse missing values, multiple imputation of missing variables reduces bias relative to deleting incomplete cases in a dataset because complete case data often differs systematically from incomplete case data (Little & Rubin 1987; Schafer 1997). Thus, case-deletion is not advisable in most instances. Moreover, in multivariate analyses such as ours, case deletion results in data being discarded, not only causing bias, but also an unacceptable loss of power.

27. "Finally, the year of collection of the drilling and felling data should be reported. There could, after all, also be temporal shifts in stem rot frequency or severity with anthropogenic global change considering changes in climate, nutrient availability, etc."

Response: Felling and drilling observations and associated soils data were collected in 1969-1971. We have added this date to methods section 2.2. We have no way of evaluating the influence of global climate change on stem rot infection, so we do not address this topic in our manuscript.

C3956

28. "The calculation of the plot level proportion of stem biomass lost to stem rot fails to account for the sampling biases inherent in variable radius plot designs. Variable radius plots sample a higher area for large trees than for small trees, and given that large trees also have a higher proportion of stem rot, the current calculations will overstate the biomass lost to stem rot at the plot level. This bias can be entirely removed by using standard expansion factors based on the measured diameters of every tree, and this is what should be done."

Response: We are open to more discussion on this point, but currently we do not understand how the variable size of the plots should bias our stand-level stem biomass loss metric, Lossmax, which is expressed as a percent, not per unit land area. If we incorporated the actual land area sampled using expansion factors, area would cancel out of the equation, since the same trees, regardless of their sizes, are being considered in both the numerator and denominator of the equation below:

$$\text{Max Stem Biomass Lost/Area} \div \text{Total Biomass /Area} = \text{Max Stem Biomass Lost / Total Biomass}$$

Given that these trees were the trees sampled, Lossmax therefore has no bias due to not using expansion factors. The only possible bias that could be introduced using prism sampling is that the trees themselves were not randomly chosen for sampling, although the locations for the centers of the prism plots were. However, we note that prism sampling is a commonly used forestry method. Moreover, while our Lossmax estimator may over-estimate stem biomass lost to rot due to possible over-sampling of large trees, the amount by which it is an over-estimate is small, because most biomass in a forest is contained in the large trees, not the small trees. In other words, the small trees contribute less to biomass, so any error from their under-sampling is small and would have little total effect on the stand-level Lossmax. Our estimates of stem biomass lost to stem rot would comprise some of the only such estimates in the literature that are based on such an extensive level of taxon sampling and such thorough methodology, and so they are valuable. Additionally, our unit of measurement for Loss-

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max is cluster, which is a group of nine prism plots. Therefore, using expansion factors to calculate stem biomass lost per hectare would not be possible. If we modified our analysis to evaluate stem biomass at the plot level, the expansion factors would be unreliable because not all trees were selected for felling. While "cluster" is not a defined unit of area, it is clear from Figure S3 that soil chemistry in terms of soil PC values varies much more among clusters than within clusters. Our objective was to scale soil-based effects of stem stem rot that we observed in individual trees to the stand-level by aggregating the stem biomass loss over many trees growing on a similar edaphic habitat. Our intention was not to create a quantitative, per land area measure of stem rot lost to biomass. Instead, our goal was to test whether the maximum possible amount of stem biomass lost to stem stem rot varied with soil properties, which is important for understanding determinants of the global distribution of carbon storage capacity and carbon dynamics (e.g., Yang et al. 2013, 2014). We have clarified the goals of these analyses in the Methods section 2.7 and emphasized in the Introduction the importance of understanding soil-related forest processes for estimation of global carbon dynamics.

29. "There also seems to be an inconsistency in how this loss is calculated. As it is currently done, this is really a calculation of the percent loss of merchantable stem biomass, as it only encompasses stem biomass from the base of the tree to the first branch. Given that the paper in general is more concerned with biomass, perhaps the statistic could be calculated for total tree biomass in addition to this calculation for merchantable stem biomass, although the measurements of loss are based exclusively on the merchantable stem biomass. If only stem biomass loss is calculated, then perhaps the statistic should be referred to somewhat differently"

Response: Please see the response to comment #6.

30. "The particular choice of statistical analyses to explain variation in stem rot among trees and plots was not motivated, and I'm not convinced the approach taken was the best. And regardless of the approach taken, the manuscript or supplemental materials

C3958

should report the fitted coefficients of the best models: these coefficients embody a considerable amount of the knowledge gained from this study.”

Response: We are happy to include tables of linear model coefficients of revised analyses (see response to comment #31 below for details) in supplementary material provided during manuscript revision.

31. “The analysis at the tree level excludes species with 5 or fewer individuals, which has a big effect on sample size, as the number of analyzed samples is just 661 of 1035 felled trees, and 616 of 1780 drilled trees (comparing Table 1 with the methods text).”

Response: Deleting species represented by five individuals or fewer was not the main contributor to the reduction in sample size in the drilling and felling datasets. The vast majority of omitted observations were because of either missing species-level covariates or missing soil information. After observations lacking model covariates that could not be imputed were deleted from each dataset, a relatively smaller proportion of observations (10% in the felling and 15% in the drilling) were excluded because they lacked five individuals per species. We had originally used this threshold of 5 trees/species to alleviate model convergence problems we experienced in PROC GLIMMIX in SAS. However, we have been able to avoid convergence errors using the glmer and lmer packages in R, so we would be happy to present these model fits obtained in R that include rare species in a revised MS.

32. “In terms of the statistical approach, why not use multimodel inference to determine the best model, which seems like it will not include two of the soil PCA variables, etc.?”

Response: In fact, we used AIC-based model selection approaches to eliminate higher order interactions not explaining significant variation in stem rot response variables (see section 2.6, page 12, line 10). To allow comparison among datasets, however, we chose to present models including all main-effects covariates tested, even if they were not statistically significant. In revised data analyses using R packages for fitting generalized linear mixed effects models (see the response to comment #31), we con-

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ducted stepwise removal of interactions and covariates from models and AIC-based model comparison find the most-supported model. In all cases in the revised analysis, models including soil PC3 had lower AIC values, and by virtue of the likelihood ratio test, were considered better models than models without soil PCs. Consequently, all analyses so far point to the association of stem rot with edaphic variation. We are happy to include these revised analyses in a revised manuscript, and to update the associated figures and tables to reflect these changes to the core analyses.

33. “It would be nice to see the fitted relationships for probability of stem rot vs. diameter in the three datasets. At least in supplemental materials..”

Response: We will be happy to provide figures showing the fitted relationships in a revised version of our manuscript.

34. “The fitted model was apparently linear in dbh; is this functional form supported by examination of residuals?”

Response: The residuals vs. DBH relationship met the assumption of linearity for generalized linear model analysis using a binomial error distribution with a logit transformation. We also tested models with higher order polynomials of DBH, and these models had higher AIC than the linear DBH model, demonstrating that a non-linear function of DBH is not supported by the data.

35. “In terms of the plot level analysis, why do pairwise analyses here, when the tree-level analyses were all multivariate?”

Response: We used multiple regression to perform the tree-level analysis because there were many tree- and species-level covariates we wanted to evaluate for their association with stem rot: species, diameter, wood density, soil habitat association, soil PC axes. Given the strong relationship between diameter and stem rot frequency, we could not evaluate any other covariate without accounting for diameter, so multiple regression was necessary. For the plot-level analysis, the only available covariates

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were the soils data (both the soil PC's and key soil variables), therefore, a bivariate approach was appropriate. Thus, we graphically depicted the results of the correlation tests.

36. "Why separately analyze correlations with six soil chemical variables as well as the four PCAs in the plot-level analysis? The whole idea of PCAs is to do these instead of the individual correlated variables; it seems inconsistent to do both PCAs and some of the individual variables. And why these 6 soil variables, anyway, out of the 30 variables that went into the PCA?"

Response: While PC axes are useful for variable reduction, they are difficult to interpret and cannot be compared across studies. The specific soil variables evaluated (pH, P, N, K, Mg, N, and Ca) were selected because these attributes are frequently measured in studies across forest sites and would thereby facilitate comparisons. There is evidence of N, P, and K co-limitation on plant growth in a lowland Panamanian forest (Wright et al. 2011) and also on root growth in a lowland Bornean forest (Kochsiek et al. 2013). Furthermore, species distributions have been associated with nutrients, such as P, Ca, and Mg, in a variety of tropical forests (Baillie et al. 1987; John et al. 2007).

37. "Finally, the interpretation of the results go beyond what can be supported. Here biomass "loss" to heartrot is calculated as the volume affected by heartrot, but this is a mix of rotted wood and void space, and the necromass and fungal biomass of rotted wood may approach the biomass of the healthy wood it replaces. As noted in the text, this complicates comparisons with other studies as this study includes all heartrot as lost, while others often look at empty volume only. Thus statements that the study here shows a rate higher than in neotropics based on comparison with neotropical studies that quantify loss as void space is not adequately supported."

Response: In general, we do not feel that the interpretation in the discussion goes beyond what is supported by the results. On section 4.1 page 18 line 25, we were careful to qualify the methodological differences between our study and previous neotropical

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surveys of stem rot (Noguiera et al. 2006; Brown et al. 1995; Clark & Clark 2000, cited in original MS). Additionally, we cite a neotropical study (Eleuterio 2011) that used chainsaw debris, not void space, to quantify rot (similar to our drilling method) as evidence that stem rot may be more prevalent in Sarawak than Amazonia. Given this evidence and the general lack stem rot data in the literature, we do not consider our statement referencing the "possible disparity in rot losses between the Paleotropics vs. Neotropics" (section 4.1, page 19, line 2) to be too outlandish. We have added text in the Discussion to reinforce the perhaps obvious point that our study was observational and that further studies are required in order to corroborate whether the patterns we observed in our study hold across multiple tropical forest systems. Furthermore, we question the idea that necromass plus fungal biomass in rotting heartwood would approach the biomass of healthy wood. Mass loss is intrinsic to the process of decomposition because CO₂ is released via respiration as decomposers metabolize the carbon in plant tissue. It is not evident that the mass lost from decomposing wood is completely made up by the growth of the fungal biomass, especially since the development of stem rot is a complex process occurring over many years and involving many continuous changes. While estimates of biomass loss rate due to heart rot in still-living trees are rare, studies of standing dead trees indicate approximately exponential biomass loss over time (Harmon et al. 1982, Lang & Knight 1979). Therefore, while we cannot quantify the exact amount of biomass lost to rot in the trees felled in central Sarawak, it should not be controversial to suggest that the density of biomass in rotten sections of wood is less than the density in intact sections. We have modified section 4.4 of the discussion to emphasize the inherent qualitative difference in mass between rotten and intact wood.

38. "The discussion also suggests that the differential loss of biomass to heartrot in different sites would affect the quality of biomass estimates. This is certainly true for standard allometric equations. The text implies the problem would be even worse for LiDAR-based estimates (page 6844). I see no basis for this claim, as lidar-based biomass estimates are typically calibrated against the same tree-based allometric

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equations used for plot-based estimates. This claim needs to be either justified or dropped.”

Response: It was perhaps inaccurate to say that LiDAR-based estimates would be “worse” because the estimates are stemming from the same allometric equations. This sentence can be dropped from a revised manuscript, as it is not essential to our argument that the accuracy of forest biomass estimates requires accounting for stem rot.

39. “6841 – 27-29. Text reads “Lower nitrogen concentrations in wood and soil may also cause wood-decay fungi on low fertility soils to excavate greater volume of wood to satisfy nutrient requirements (Boddy, 2001).” The logical complement of this would be to say that higher nitrogen concentrations in wood and soil cause wood-decay fungi to excavate less wood, i.e., to grow less – which makes no sense whatsoever. In general higher resource levels leads to more proliferation of the organism consuming the resource, not less.”

Response: We clarify the above sentence to read: “Wood decay-fungi, which contribute to the formation stem rot, often originate from long-lived mycelia in the soil (Boddy et al. 2001). Consequently, the quantity of wood excavated at given site may depend on the relative availability of limiting elements in soil vs. woody biomass, and, as a consequence, wood may be a more attractive substrate where soil is poor in nitrogen and phosphorus.”

40. “Table 4 – A key piece of information is missing here. What is the total explained variation? At the least this should be given here for reference for each analysis. To me, it would be even more useful to normalize the listed percentages by this value, so that the table showed percent of total variation explained by each factor, rather than the percent of explained variation.”

Response: Currently, statisticians have not settled on a consensus calculation for the total model variance explained by mixed effect models (Nakagawa & Schielzeth 2013). We present pseudo-R² values section 2.6 page 12 line 17 in to give an approximation

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of the proportion of total variance explained by the model, however, this value cannot be directly applied to variance partitioning values, especially since they contain different covariates. The goal of the variance partitioning analysis was to the relative importance of model covariates.

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Please also note the supplement to this comment:
<http://www.biogeosciences-discuss.net/12/C3941/2015/bgd-12-C3941-2015-supplement.pdf>

Interactive comment on *Biogeosciences Discuss.*, 12, 6821, 2015.

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